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New World thermometer crickets: the *Oecanthus rileyi* species group and a new species from North America

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Abstract

Oecanthus alexanderi n. sp. Walker occurs in the lower Rio Grande valley of Texas and in Mexico as far south and west as Michoacan. Its song and morphology establish it as a member of the *Oecanthus rileyi* species group. Other members of this group of New World species include *O. rileyi* Baker, *O. allardi* Walker & Gurney, and *O. fultoni* Walker. Calling songs of the *rileyi* group consist of chirps or brief trills in which trios of pulses are produced in such rapid succession as to be indistinguishable to the human ear. The chirps/trills are easily countable and have a highly regular rate that varies linearly with temperature. Extrapolated regression lines tend to converge at 4°C and an expected chirp rate of 0. Because of these relations, simple formulas can convert counts of chirps vs time into surprisingly close approximations of ambient temperature—justifying the group's designation as "thermometer crickets".

Key words

Gryllidae, Oecanthinae, temperature effects, calling songs, *Oecanthus allardi*

Introduction

The 62 described species of the genus *Oecanthus* are broadly distributed in temperate and tropical regions around the world (Eades & Otte 2010). Of the 26 New World species, Walker (1967) placed *rileyi*, *allardi*, and *fultoni* in the *Oecanthus rileyi* group. These species have a round or oval dark mark on an ivory swelling on the ventral surface of each of the first two antennal segments, and their calling songs consist of chirps or brief trills produced at a highly regular rate. Within each chirp or trill, the pulses, which correspond to individual tegminal closings, occur in groups of three, except that the first group usually has two pulses rather than three.

In May of 2009, one of us (NC) organized a field trip to find two species of Oecanthinae known in the United States only from the lower Rio Grande valley and not collected there in more than 50 y. NC, accompanied by Laurel Symes, a Dartmouth College graduate student interested in tree crickets, failed to find the two target species, but NC recorded an unfamiliar tree cricket call in two counties and heard it in a third. When TW heard the recordings, he concluded the song was produced by an undescribed species of the *O. rileyi* group and soon realized that the song was among the tree cricket calls that R.D. Alexander had recorded in Mexico in 1965 and had asked TW to study. In June 2009, NC returned to the lower Rio Grande and collected one male.

This paper describes, as *Oecanthus alexanderi* n. sp., the species that NC recorded and collected and updates and organizes what is known of the songs of the *rileyi* species group and their usefulness for estimating temperatures in the field.

Methods

Morphological measurements.—All specimens had been preserved in alcohol. Measurements >10mm were made with a dial micrometer. Those ≤10mm were made with the ocular micrometer of a stereoscopic microscope. To facilitate measuring the length of the stridulatory file and counting its teeth, the right tegmen was excised.

Song recording and analyses.—In 29 May to 14 Jun 1965 fieldwork in Mexico, R.D. Alexander [RDA], assisted by R.T. Vinopal, used a Nagra tape recorder to record calling songs of many oecanthines. Subsequently RDA used a Kay Vibralyzer audiospectrograph to analyze the songs and loaned his analyses and some accompanying specimens to TW for study. TW reported to RDA that the material evidenced the existence of several undescribed species of the *Oecanthus rileyi* group, but neither RDA or TW pursued the matter at that time.

NC recorded songs with a Canon PowerShot S5 IS digital camera set in video mode at 30 frames/s, with the camera held as close to the cricket as feasible. The sound track was 16 bit with a sampling rate of 44,100 Hz. The 1.5×1 cm, wire-mounted probe of an Acu-Rite model 00891 digital thermometer was used to measure temperatures. Its accuracy was confirmed by comparing, in a water bath, its readings with a precision glass laboratory thermometer. Temperatures for the recordings of the holotype were made with the probe 5 to 15 cm from the subject.

An avi-to-wav converter marketed online by 008soft.com was used to extract the sound track from the video file. We used Cool Edit 2000 (Syntrillium Software) to analyze the sound tracks and to make images of their wave forms. Dominant frequency of a call was determined to the nearest 0.1 kHz by using FIT frequency analysis to determine the peak frequencies of a series of individual chirps and accepting the mode of the values obtained. Chirp rate was determined from the duration of the longest available sequence of regularly produced chirps, as measured from the start of the first chirp to the start of the last. That measurement was then divided by the number of chirps within the measured time interval. Within a chirp, average pulse rate was determined to the nearest 0.1 p/s by measuring from the start of the first clearly defined pulse to the start of the last. If the ends of the pulses within the chirp were more clearly defined than the starts, ends were used. In either case, the measurement was then divided by the number of pulses within the measured time interval. Average pulse rate within a recording was calculated as the average of the intrachirp pulse rates of three or more successive chirps.

The University of Michigan Museum of Zoology [UMMZ] loaned the Borror Laboratory of Bioacoustics the reels of tape recordings from RDA's field work that were relevant to our study. The Borror

Laboratory sent digitized versions of some of these reels to TW, who used Cool Edit 2000 to analyze the songs of species of the *rileyi* group. UMMZ also loaned TW the *Oecanthus* specimens collected by RDA during his Mexican field work.

Recordings of Oecanthus allardi.—Four recordings of *O. allardi* were analyzed to broaden what was known of the calling songs of that species: MLNS#133699, Port-au-Prince, Haiti, 25.8°C; MLNS#114402, Milk River Bath, Jamaica, 26.8°C; MLNS#113506, Cobo Rojo, Puerto Rico, 24.0°C, and WTL#1992-19, Montserrat, BWI, 26.2°C. All were initially in the Walker Tape Library (WTL), but the first three had later been digitized and archived by the Macaulay Library of Natural Sounds (MLNS) at Cornell University. Analysis was with Cool Edit 2000 and rates were adjusted to 25°C by assuming that the temperature at $\hat{y}=0$ was 4°C (as explained later in this paper).

Trend lines for chirp rates.—Trend lines for depicting chirp rate as a function of temperature were generated from XY data sets using the least-squares, linear-regression charting function of Excel 2007 (Microsoft). To obtain XY data sets for *O. fultoni* in Iowa and Oregon and for *O. rileyi* in Oregon (Fulton 1925, Figs 4 and 5), data points on enlarged versions of the published scatter plots were converted to numbers from measurements made with a millimeter rule. The r^2 of the trend line for *O. fultoni* in Ohio (Walker 1962, Fig. 12) was not available. To obtain one, the XY data set was recreated from an enlarged version of the figure. [These four recreated data sets and trend-line calculations are in Supporting Materials.]

Results

Oecanthus alexanderi Walker, n. sp.

Figs 1-3, video and photographs in Supporting Material

Holotype.—Male; Bentsen-Rio Grande Valley State Park, Hidalgo County, Texas, 7 Jun 2009, N.J. Collins, collr; Texas A&M Univ. Collection. Body length 15.6 mm; tegminal length 19.0, width 6.1;

pronotal length 2.1, rear width 2.3; hind femur 7.6. Ventral markings on first two antennal segments as in Fig. 1. Song as in Fig. 2 and Table 2. A video and photographs of the living holotype are in Supporting Material.

Paratypes.—University of Michigan Museum Zoology. MEXICO. **San Luis Potosi:** 1 male (UMMZI-00226529), ca 30 mi E Ciudad del Maiz, 1 Jun 1965, RD Alexander, RT Vinopal; 2 males (UMMZI-00226557), 25 mi W Ciudad Valles, 21 Oct 1966, RD Alexander. **Michoacan:** 1 male (UMMZI-00226530), Tuxpan, 10 Jun 1965, RD Alexander, RT Vinopal.

Habitat.—NC has recorded the song or collected *O. alexanderi* from a *Hibiscus* bush and on Turk's Cap (*Malvaviscus arboreus*), both on the grounds of the headquarters of the Bentsen-Rio Grande Valley S. P., and on sunflower (*Helianthus annuus*) at the edge of closed canopy woods in Resaca de la Palma S. P., Cameron County, Texas. This might generalize to disturbed areas of mixed growth forms. No specific information on the habitat of the species in Mexico is available.

Calling song.—The slower chirp rate and longer chirps immediately distinguish the calling song of *O. alexanderi* from those of the other two species of U.S. tree crickets whose calls are low-pitched (<3kHz), highly regular, continuous series of melodious chirps. Indeed, R.D. Alexander, for whom the species is named, dubbed it "very slow [*Oecanthus*] *fultoni*" when he first heard it during his Mexican field work in 1965. Figure 2 shows the structure of the song at three resolutions: 2A illustrates the highly regular chirp rate; 2B shows the characteristic grouping of pulses within chirps (which makes them tremulous to the human listener); and 2C shows the sound envelope of a single chirp. Table 1 quantifies the physical properties of recordings made of the holotype and of two field recordings. A video of the holotype calling is in Supporting Materials.

In Fig. 3, the five determinations of chirp rates for Mexican *O. alexanderi* are by RDA as given to TW in 1966 and are from Michoacan (Tuxpan), Tamaulipas (Ciudad Victoria), and San Luis



Fig. 1. Antennal markings of holotype of *O. alexanderi*. For color version, see Plate XIV.

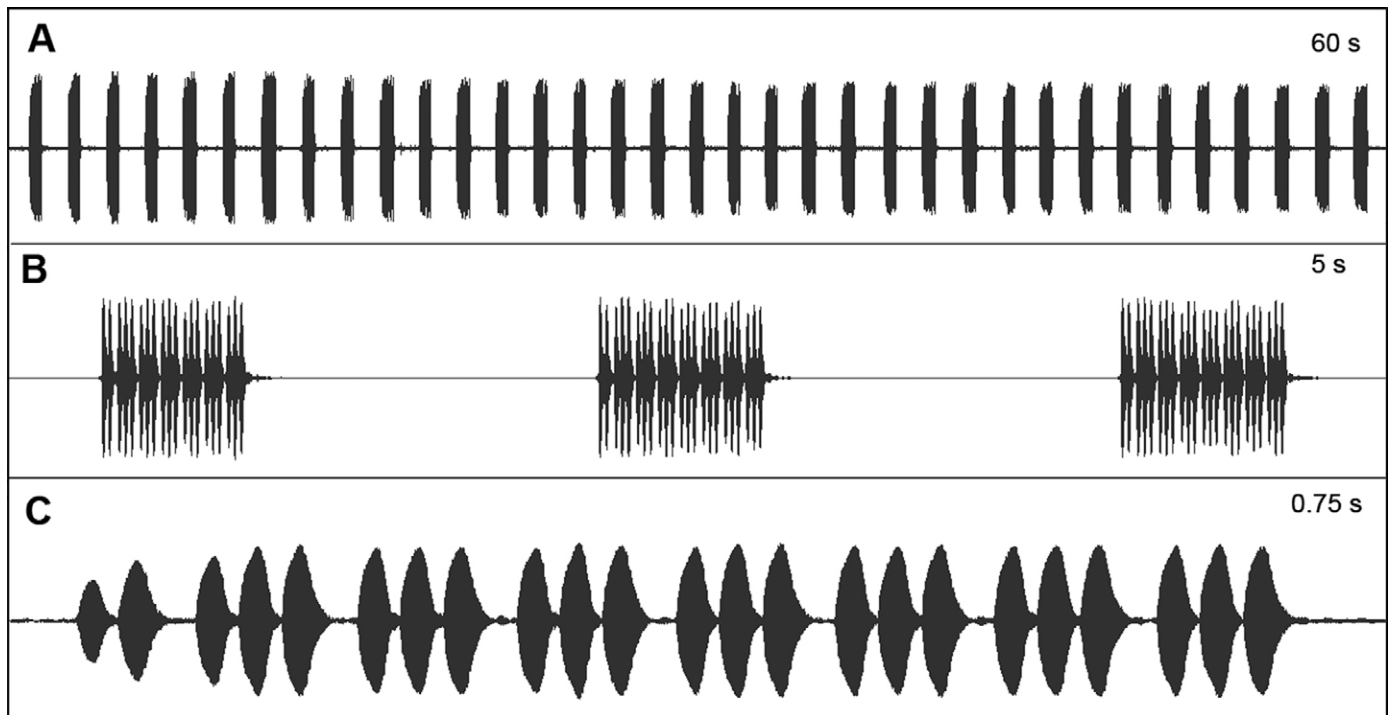


Fig. 2. Waveforms of the calling song of *O. alexanderi*. A. One minute of calling by holotype at 22.9° C: 35 chirps (WTL575-3-c). B. 5 s of calling of holotype at 23.2° C; three successive chirps: the first with 20 pulses, the others with 23 pulses (WTL575-3-b). C. One 23-pulse chirp recorded at type locality (WTL575-1).

Potosi (30 mi E Ciudad Maiz). When TW analyzed for chirp rate the digitized versions of two recordings assumed to be the basis of Mexican data in Fig. 3, the rate for 23.9° C (San Luis Potosi) was 4 ch/min faster than the figure given him by RDA and the rate for 27.2° C (Tamaulipas) was 6 ch/min slower. Because of the poor quality of the digitized versions (made 45 y after the original analog versions), no other verifications of the original chirp-rate determinations were attempted. The only digitized song of Mexican *O. alexanderi* suitable for intra-chirp analysis (RDA65(10)-1 from San Luis Potosi) had an average pulse rate of 48.6 at 23.9° C and 6 of the 7 chirps consisted of 20 pulses.

Song comparisons within the O. rileyi species group.—The most evident differences in the calling songs of the four species in the *rileyi* group are in chirp rate (Fig. 3), but differences in chirp duration are also easily heard. In Table 2, a useful proxy for chirp duration is the number of pulses per chirp. (Pulse rate also changes chirp duration, but differences in pulse rate are relatively minor and are in the direction that increases the effects of pulse number on pulse duration—*i.e.*, faster pulse rates occur in the species with lower numbers of pulses per chirp.)

Fulton (1925) and Walker (1962a) determined the chirp rates of *O. fultoni* and *O. rileyi* over broad ranges of carefully measured, sometimes controlled, ambient temperatures. For *O. fultoni*, Fulton showed that the population he studied in Oregon had a substantially higher chirp rate than the one he studied in Iowa (Fig. 3). Walker (1962a) could not distinguish the chirp rates of two *O. fultoni* populations in Ohio from those that Fulton had studied in Iowa and showed that chirp rates of *O. rileyi* at four localities in California and one in Oregon were compatible with Fulton's data from Corvallis, Oregon. When the trend lines from these four data sets are plotted, their downward extrapolations converge most closely where the value of expected chirps per minute (\hat{y}) is 0 (Fig. 3). The mean temperature at $\hat{y}=0$ is 4.0 and the range is 3.5 to 4.7° C (Table 3).

Allard (1957) studied the chirp rates of *O. allardi* in the Dominican Republic over a range of about 6° C. The range for *O. alexanderi* recordings in Texas at known temperatures is less than 5° C (Table 1 and Fig. 3). The calculated trend lines for these two species have temperatures at $\hat{y}=0$ of 0.7 and 0.3° C. If the trend lines for these two species are constrained to pass through 4.0° C at $\hat{y}=0$ (the mean value for the other four trend lines in Fig. 3), it does little to alter

Table 1. Recorded calling songs of *O. alexanderi*.

WTL no.	Date	Locality	Temp (°C)	Peak freq (kHz)	Average pulses s ⁻¹	Chirps min ⁻¹	Pulses/chirp (mode)	Notes
Indoors (holotype)								
575-3-a	13-Jun-09	Hildalgo Co., TX	27.5	2.6	47.2	40.7	~19	11 s, 5 then 6 chirps
575-3-b	14-Jun-09	Hildalgo Co., TX	23.2	2.3	38.0	31.9	23	15 s, 8 chirps
575-3-c	14-Jun-09	Hildalgo Co., TX	22.9	2.4	39.0	35.1	20	94 s, 55 chirps
575-3-d	14-Jun-09	Hildalgo Co., TX	23.3	2.4	39.2	35.2	23	26 s, 15 chirps
Outdoors								
575-1	18-May-09	Hildalgo Co., TX	?	2.3	?	29.4	23	11.4 s, 5 chirps
575-4	16-May-09	Cameron Co., TX	?	2.4	?	33.9	20	9 s, 5 chirps

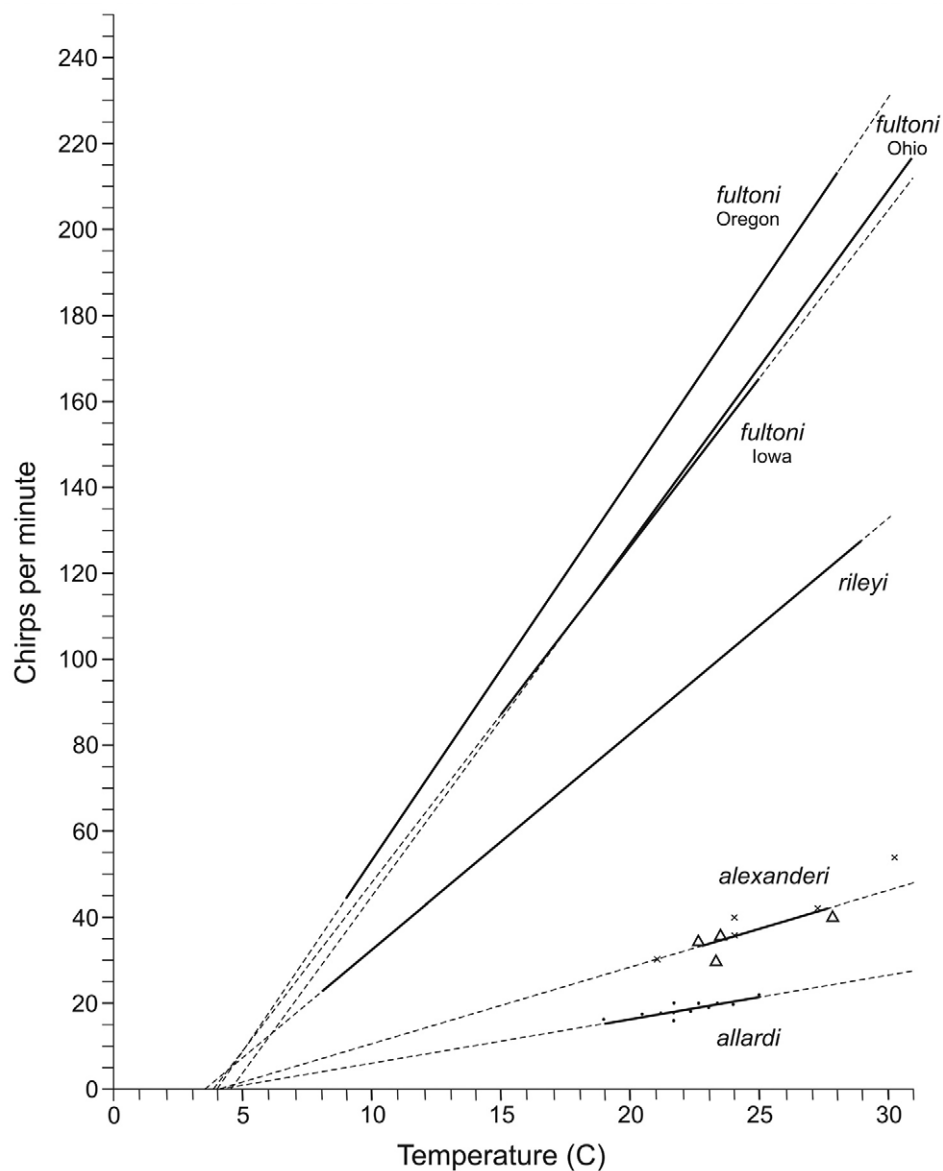


Fig. 3. Chirp rates of species in the *O. rileyi* species group. Lines are based on the formulas in Table 3. The solid portions of the lines show the range of the data used to determine the formulas; the dashed portions are extrapolations. For *O. alexanderi* and *O. allardi*, the data points used to calculate the lines are shown by triangles and dots respectively. Because the data for these two species are from a narrow range of temperatures, the calculated lines were constrained to pass through 4.0°C at $\hat{y}=0$ (see text). The x's are RDA's data for Mexican *Oecanthus* that are here classified as *O. alexanderi*.

the fit of those lines to their respective data sets (Fig. 3). Specifically, the r^2 value for the *allardi* line changes from 0.697 to 0.674, and for the *alexanderi* line it changes from 0.804 to 0.778 (Table 3).

Discussion

Morphological distinctions among species.—Discovering new morphological differences among the species of the *rileyi* group was not among the goals of this paper as defined in its Introduction. However, when sought, morphological differences among species of the *rileyi* group have been found in the male genitalia of *allardi*, *fultoni*, and an undescribed species (Walker & Gurney 1960) and between the antennal markings of *fultoni* and *rileyi* (Walker 1962a). When Walker and Gurney (1967) studied the male metanotal gland for taxonomic value among U.S. *Oecanthus*, they found the features of the gland useful in separating the species into major groups, but not in separating otherwise similar species. With one exception, species groups based on features of the metanotal glands corresponded to the ones that Walker (1962a, 1963) had earlier established based on other features. The exception was that *fultoni* and *rileyi* differed from the other members of Walker's (1962a) *Oecanthus niveus* group. On

this basis Walker and Gurney (1967) recognized the *O. rileyi* group as distinct from the *O. niveus* group. They also noted that *O. fultoni* showed significant geographical variation in the structure of the metanotal gland between West Coast and eastern populations.

Block's data set for O. fultoni.—In 1966, B. C. Block published extensive data on the chirp rate of *O. fultoni* as measured outdoors with a stopwatch on the campus of Pennsylvania State University in University Park, Pennsylvania. These were not made part of Fig. 3 and Table 3 because they were not as tightly clustered around a trend line for eastern U. S. *O. fultoni* as were the data for Iowa and Ohio. The Iowa line (Fulton 1925) was from a single male calling indoors, where temperatures are more stable than outdoors, and the Ohio line (Walker 1962) was from a set of males recorded individually in the laboratory under controlled temperatures. The r^2 values for these trend lines range from 0.959 to 0.993, compared to 0.906 for Block's data. Higher r^2 values should increase the precision of the values determined by extrapolating trend lines downward to $\hat{y}=0$. Nonetheless, Block's data set shows a linearity and slope similar to the other two lines [p. 5, Supporting Materials; temperature 3.2°C at $\hat{y}=0$].

Table 2. Calling song features in the *O. rileyi* species group with rates adjusted to 25°C. Species in this group produce regularly spaced chirps that characteristically start with an initial pair of pulses followed by one or more trios. CR=chirp rate, PR=pulse rate, CF=carrier frequency, ND=no data. Sample sizes for the values in this table are in the sources. The table's last four lines are each based on a single recording, three of which are currently available online.

Species	Localities	CR min ⁻¹	PR s ⁻¹	CF kHz	pulses/ch (mode)	Source
<i>O. fultoni</i>	Oregon, California	195	52	2.6	5-8 (8)	Fulton 1925, Walker 1962a
<i>O. fultoni</i>	Ohio	167	52	2.6	5-8 (8)	Walker 1962a
<i>O. rileyi</i>	Oregon, California	111	47	2.6	8-14 (11)	Fulton 1925, Walker 1962a
<i>O. alexanderi</i>	Texas	37	42	2.5	17-23 (23)	this paper
<i>O. allardi</i>	Dominican Repub.	22	ND	ND	ND	Allard 1957
<i>O. allardi</i>	Puerto Rico	21	43	2.6	20-26	MLNS#113506
<i>O. allardi</i>	Haiti	19	39	2.6	26-44	MLNS#133699
<i>O. allardi</i>	Jamaica	20	40	2.7	30-35 (32)	MLNS#114402
<i>O. allardi</i>	Montserrat	21	42	2.7	19-28 (25)	WTL#1992-19

Chirp rates and cricket thermometers.—If one were to assume that 4°C was the temperature at $\hat{y}=0$ for all chirp-rate trend lines for populations of species in the *O. rileyi* species group, a single chirp-rate datum at a single temperature would allow the trend line for the population to be estimated and formulas to be calculated for using the songs of the population to estimate the ambient temperature of the singer. The 4°C value is derived from only four calculated trend lines (Fig. 3, Table 3). However, studies of the relationships of pulse rate and temperature in ten species of North American *Oecanthus* support the possibility that a larger sample would produce a similar value. Unlike chirp rates, pulse rates in crickets are nearly always too rapid to measure by counting units with stopwatch in hand, but the rates are easily determined with electronic audio recording and analyzing devices. Walker (1962b, Table 1) concluded that in the case of ten species of *Oecanthus*, the relation of pulse rate to temperature was linear and found that for the extrapolated trend lines the mean of the temperatures at $\hat{y}=0$ was 4.1±1.1°C (mean±SD).

Given the above considerations, it is possible to create a formula for estimating temperature from a trend line or even from a single XY data pair. Below is how the latter may be done. The XY data pair used to exemplify the procedure will be 112 chirps min⁻¹ at 25°C (or 77°F) — as in *O. rileyi*.

1. A trend line based on any single data pair connects the data pair with the hypothetical data pair of 0 chirps min⁻¹ at 4°C (or 39°F).

2. Because seconds (s) are the unit of time in temperature-estimating formulas, convert ch min⁻¹ to ch s⁻¹ [112ch min⁻¹/60 = 1.87ch s⁻¹].

3. To calculate the slope of the trend line (*i.e.*, the change in chirp rate for each 1° change in temperature) determine the number of degrees between the temperature of the initial data pair and the temperature at $\hat{y}=0$ [25-4=21°C or 77-39=38°F]. [Because the expected chirp rate drops to 0 in this span of temperature, the change in chirp rate is 1.87 ch s⁻¹ and the slope is either 1.87/21=0.089 (for C) or 1.87/38= 0.049 (for F).]

4. The simplest formula for temperature estimation is to count the chirps in *n* seconds and add the temperature at $\hat{y}=0$, where *n* is the reciprocal of the slope. [For C, that would be the chirps in 11.25 s and add 4. For F, that would be the chirps in 20.4 s and add 39.]

5. With manual timing, accurately counting chirps in brief, exact time periods is impractical. To facilitate field estimation of temperature from species with slow chirp rates, formulas with longer periods for counting can be derived from the basic ones. For example, "Count the number of chirps in 45s, add 16, and divide the sum by 4" will yield the Celsius temperature in the current example.

When applied to any point in the trend line for the song of *O. alexanderi*, the above procedure yields these two temperature-estimating formulas: for Celsius degrees count the number of chirps in 33 s and add 4. For Fahrenheit degrees, count the number of chirps in 60 s and add 39.

Other thermometer crickets.—The only Old World crickets that have been studied carefully as potential thermometers are, like those in the New World, members of the genus *Oecanthus*. Toms (1992), in considering candidates among African crickets, reviewed the requirements for cricket thermometers and noted that most crickets have rates within their calls that have a highly predictable, linear relation to the ambient temperature of the caller, but that these rates are generally wing-stroke rates (pulse rates) and are too fast to quantify by ear. He also noted that rates that are easily countable, such as many chirp rates, are rarely among those that are highly predictable in their relation to temperature and that thermometer crickets need to be easily heard and should broadcast from a place well exposed to changes in air temperatures, rather than on the ground or in a burrow. For these reasons he focused on three species of African *Oecanthus* that produce chirps at regular rates. One of these (*O. sycomorus*) produces chirps at a rate too high to be counted (>8 s⁻¹), but the other two (*O. karschi* and *O. capensis*) produced

Table 3. Trend lines for chirp rates of species in the *Oecanthus rileyi* species group.

Species	Locality	Temp range (°C)	b	a	r ²	°C at $\hat{y}=0$	Source
<i>fultoni</i>	Iowa	15-25	7.7879	-30.21	0.993	3.9	Fulton 1925
<i>fultoni</i>	Oregon	9-28	9.2007	-36.53	0.959	4.0	Fulton 1925
<i>fultoni</i>	Ohio	18-31	8.208	-38.61	0.970	4.7	Walker 1962a
<i>rileyi</i>	Oregon	8-29	5.2025	-18.08	0.991	3.5	Fulton 1925
<i>alexanderi</i>	Texas	23-28	1.4963	-0.52	0.804	0.3	this paper
			1.7645	-7.06	0.778	4.0	if x=4.0 at $\hat{y}=0$
<i>allardi</i>	Dom. Rep.	19-25	0.8693	-0.58	0.697	0.7	Allard 1957
			1.0264	-4.11	0.674	4.0	if x=4.0 at $\hat{y}=0$

chirps at usable rates ($<4\text{ s}^{-1}$) (Toms & Otte 1988). Toms (1992) concluded that the latter two species had about the same reliability as thermometers as *O. fultoni*. However, he based his estimate of the reliability of *O. fultoni* on the data set of Block (1966) which was based on outdoor measurements of the ambient temperature at 4 ft from the calling crickets. Changes in outdoor ambient air temperatures over small distances and brief time intervals make it difficult to determine the temperature where and when the cricket is calling. In contrast, the trend lines for eastern U.S. *O. fultoni* in Table 3 are based entirely on indoor temperatures, measured close to the calling cricket and have much higher r^2 values than the one for Block's data (see above).

Toms (1992) showed that the extrapolated trend lines of chirp rate vs temperature for the three African *Oecanthus* he studied tended to converge at $\hat{y}=0$, but at 9°C rather than the 4°C established for the *rileyi* species group. Walker (1975) reported similar differences among the mean convergence temperatures for other taxonomic groups of crickets and katydids.

Accuracy of cricket thermometers.—Plots of pulse and chirp rates of oecanthines as functions of temperature are remarkably linear even when (1) ambient temperature is not carefully controlled and (2) multiple individuals from the source population are not distinguished in the data set (Walker 1962a, 1963; Toms & Otte 1988; Toms 1992). In the literature on thermometer crickets, these two sources of variation have been simultaneously minimized only once—Fulton's (1925) chirp-rate data for a single individual of Iowa *O. fultoni* (first entry in Table 3 and p. 2 of Supplementary Material) with an r^2 value of 0.993.

On the other hand, we are obliged to point out that no study of any population of thermometer cricket (New World or Old) has statistically defined the accuracy of the responses of individuals to carefully controlled ambient temperatures, nor has any study statistically defined the intrapopulation variation in these responses. Finally, we must mention that individuals calling within hearing range of one another may change their chirp rates to achieve synchrony (Walker 1969).

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